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Range expansion of an invasive species through a heterogeneous landscape – the case of American mink in Scotland

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ABSTRACT

Aim The impact of invasive species is one of the main causes of biodiversity loss world-wide, and as a result, there is much interest in understanding the pattern and rate of expansion of species outside their native range. We aimed to characterize the range expansion of the American mink (*Neovison vison*) invading from multiple introduction points through a varied landscape bounded by coastline to better understand and manage its spread.

Location Scotland, UK.

Method We collated and used records of mink presence to calculate the historical range and rate of range expansion at successive time intervals. We used a presence-only model to predict habitat suitability and a newly developed individual-based modelling platform, RangeShifter, to simulate range expansion.

Results Records showed that mink were distributed throughout Scotland, except in the far north. We found that the rate of spread varied both spatially and temporally and was related to landscape heterogeneity. Habitat suitable for mink in west Scotland is restricted to the coast.

Main conclusions We concluded that temporal and spatial variation in range expansion is attributable to heterogeneity within the landscape and also demonstrated that the potential for long-distance dispersal does not necessarily facilitate range expansion when availability of suitable habitat occurs in narrow strips and/or is fragmented. We have highlighted methodological gaps in calculating rates of expansion in invasive species but have demonstrated alternative methods that successfully utilize presence-only data. Our study reaffirms that invasive species will colonize less favourable habitats and highlights the need to remain vigilant of their potential for expansion even when distribution appears to be static for a time.

Keywords

American mink, biological invasions, habitat availability, heterogeneous landscape, invasive species, multiple introduction points, range expansion.

INTRODUCTION

The impact of invasive species is one of the main causes of biodiversity loss world-wide (Genovesi, 2009) which has resulted in great interest in understanding patterns and rates of expansion of species outside their native range. Classic diffusion theory typically considers scenarios of symmetrical, radial expansion from a central point, the speed of which are determined by the dispersal ability and reproductive rate of the population (Skellam, 1951). Expansion of the species range across the radius of the circle (the radial invasion range) theoretically occurs either at a constant rate increasing

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linearly with time, at an initially slow, but secondarily higher rate, or at an accelerating rate, where the distance gained increases each year (Shigesada *et al.*, 1995).

Empirical examples of constant rates of range expansion are available but often fail to meet all assumptions of classic theory. For instance, expansion of the sea otter (*Enhydra lutris*) in California (a re-invading native species) occurred at a constant rate over time, but rates differed depending on the direction of movement along the linear coastal habitat (Lubina & Levin, 1988). Expansion of bank voles (*Myodes glareolus*) in Ireland proceeded at a constant rate, but although the expansion was multidirectional, it was not symmetrical because the area of invasion was bounded by coastline (White *et al.*, 2012). Complex landscapes can invoke more complicated invasion dynamics. Early predictions for the rate of cane toad (*Rhinella marina*) range expansion assumed a constant rate in a homogenous environment but were inadequate to explain the current cane toad distribution (Urban *et al.*, 2008). Cane toad spread demonstrated accelerating and decelerating range expansion in response to changing environmental conditions in the newly invaded areas (Urban *et al.*, 2008).

Advances in theoretical and empirical approaches to analysing range expansion have highlighted the importance of species interactions, evolution, long-range dispersal events, spatial heterogeneity and temporal variability as factors that can influence the invasion process (reviewed in Hastings *et al.*, 2005). Landscape structure is particularly important (With, 2002; la Morgia *et al.*, 2011) as few invaded landscapes are homogeneous and geographical boundaries can restrict the extent of the invaded range. Furthermore, whereas model studies typically focus on range expansion from a single point of introduction, multiple introductions are commonplace (e.g. Kolbe *et al.*, 2004; Miller *et al.*, 2005; Urban *et al.*, 2008; Zalewski *et al.*, 2010) and can enhance the likelihood of establishment (Sakai *et al.*, 2001). To our knowledge, model explorations, and any general understanding, of range expansion across a heterogeneous landscape bounded by coastline, from multiple introduction points are yet to be investigated.

The expansion of American mink (*Neovison vison,* hereafter mink) across their invaded range occurred through heterogeneous landscapes from multiple introduction points. Mink are small (*c.* 1 kg) carnivores imported to Europe, Asia and South America from North America for fur farming (Dunstone, 1993). Escaped and intentionally released mink have established feral populations in many countries (Bonesi & Palazon, 2007) and have had devastating impacts on several species of native birds (Craik, 1997; Nordström *et al.*, 2003; Peris *et al.*, 2009) and mammals (Aars *et al.*, 2001; Jefferies, 2003; Macdonald & Harrington, 2003; Banks *et al.*, 2008). Mink are highly mobile (Gerell, 1970) and inhabit coastal and freshwater habitats. Mink control, to benefit native species, is underway in many countries (Bonesi & Palazon, 2007). To aid mink management, the rate of spread has been estimated (Ruiz-Olmo *et al.*, 1997; Fasola *et al.*, 2011) and predicted (Iordan *et al.*, 2012). These calculations have been based on simple radial, or linear, expansion rates from isolated, single introduction points.

Management of mink in Scotland, UK, is currently in progress on a large, but not nationwide, scale (Bryce *et al.*, 2011). The current distribution of mink in Scotland originated from multiple fur farms and now encompasses a highly heterogeneous landscape of lowland agriculture, mountains, moorland and complex coastal habitats. Evidence from UK-wide randomized surveys (e.g. Green & Green, 1987, 1997; Strachan & Jefferies, 1993; Jefferies, 2003) performed to assess distribution and abundance of two species of conservation concern, the water vole (*Arvicola amphibius*) and European otter (*Lutra lutra*) that share the riparian habitat of mink, suggested that the rate of expansion of mink in Scotland has varied both spatially and temporally. However, these structured surveys only span a fraction of the duration of mink invasion. Data spanning a longer period are required to fully characterize variation and its determinants during range expansion.

This study aimed to characterize the range expansion of a species invading from multiple introduction points through a varied landscape bounded by coastline to better understand and manage its spread. The objectives of this study were as follows: (1) to calculate the observed rate of mink range expansion throughout Scotland to evaluate temporal trends in the invasion process; (2) to model habitat suitability within the Scottish landscape and relate this to expansion rate to evaluate spatial trends in the invasion process; and (3) to test scenarios relating to spatial and temporal variation in mink range expansion by simulating range expansion with a newly developed simulation platform, RangeShifter (Bocedi *et al.*, 2014). Overall, we sought to guide mink management in Scotland and apply lessons to future invasive species management.

METHODS

History of mink in Scotland

Fur farms were first established in 1938 in Scotland with the majority being located in eastern, central and southern Scotland (Cuthbert, 1973). Mink were first recorded breeding in the wild in 1962. Early distribution of mink in Scotland was mostly associated with farm location but not all farms contributed to feral populations (Cuthbert, 1973). There were strong suggestions that the distribution of mink had contracted (Jefferies, 2003) or stabilized (Strachan, 2007) by the early 2000s. Recent records suggest that the range now covers most of Scotland except the far north (NBN Gateway, 2012).

Data collection

Records of mink presence spanned 1960–2012 and were a mix of carcass (61.4%), sighting (3.5%) and field sign (10.6%) records in addition to some of unknown type (24.5%). Sources varied and included records from a

national, open access database (National Biodiversity Network, NBN Gateway, 2012), national surveys for otters and water voles that incidentally recorded mink (Green & Green, 1987, 1997; Strachan & Jefferies, 1993; Jefferies, 2003; Strachan, 2007), game bag data from sporting estates, mink management projects (e.g. Scottish Mink Initiative, SMI, 2011) and volunteer recorders. Very few data sources held records of locations where surveys took place, but mink were not found ('absence' data), precluding quantification of species detectability and observer effort. However, these systematic surveys (Strachan & Jefferies, 1993; Green & Green, 1997; Jefferies, 2003; Strachan, 2007; Harrington *et al.*, 2010) were sufficient for us to assume observer coverage beyond the reported range of mink in each decade.

Calculation of the observed rates of range expansion

Less than 10% of records were collected through structured surveys. The remainder (91%) were submitted ad hoc. Collectively the data were without doubt imperfect, showing temporal and methodological inconsistencies but were typical of data available for retrospective studies of invading species spanning several decades and large areas. The data were patchy and not expected to represent fully the observed distribution of mink in Scotland. Apparent gaps within the core of the range were unlikely to represent true absences, and conversely, unique and isolated records were unlikely to represent established populations. To account for the possibility of false-negative and false-positive records, we used probabilistic home range analyses techniques (a-LoCoH, Getz *et al.*, 2007) to quantify the likely range of mink at sequential time intervals (see Appendix S1 in Supporting Information). The 95% home range for each time step was calculated to exclude outlying observations that were potential false positives, for example recorder confusion with similar species such as native pine martens (*Martes martes*) or feral ferrets (*Mustela putorius furo*). The area of newly occupied land at each interval was then used to calculate the rate of expansion. Due to the multiple introduction points and geographical boundaries within the study area, it was not appropriate to assume, and therefore measure, radial expansion across the whole of the invaded range. We calculated the radial range expansion and rate in three segments of a quadrant (as in White *et al.*, 2012) in north-east Scotland as a sample of the invaded area that encompassed expansion through the full period of invasion and incorporated a heterogeneous landscape (Fig. 1) (see Appendix S1). Expansion in west Scotland was quantified separately because range expansion is thought to have occurred independently in western and eastern areas (Fraser *et al.*, 2013). The pattern of expansion in west Scotland was assumed to be approximately linear, with populations in the north-west originating from a south-west source (Fraser *et al.*, 2013). Additionally, we quantified area expansion across the whole invaded range in Scotland by dividing the total newly occupied area at each time interval by the number of years at each time interval.

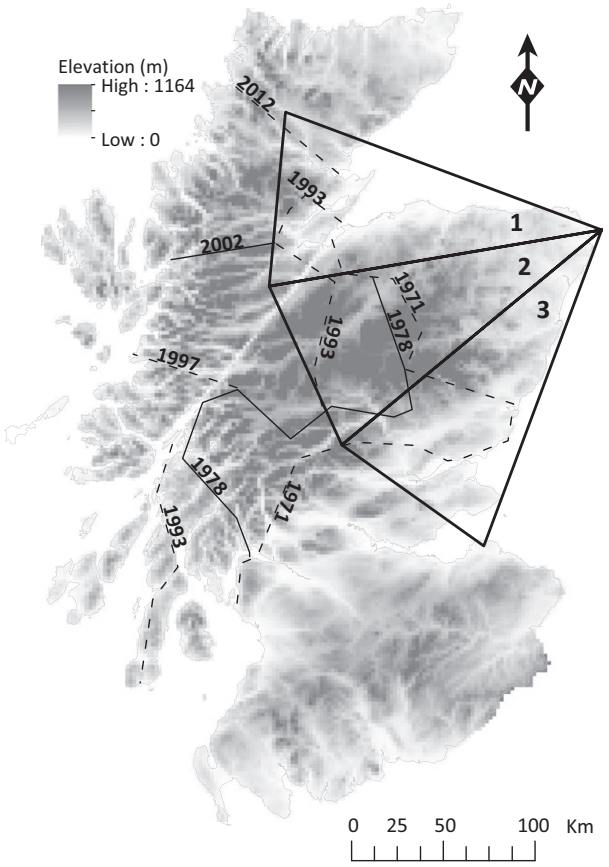

Figure 1 Summary of the study area, rough distribution of mink at sequential time intervals and placement of the three segments used to calculate radial invasion rate.

Modelling habitat suitability within the Scottish landscape

We modelled the probability of occurrence of mink across Scotland using presence-only data with the 'maxlike' method developed by Royle *et al.* (2012) (see Appendix S1). The resultant estimated occurrence probability was used as a summary of habitat suitability (Royle and Dorazio, 2008). Habitat suitability models based on presence-only data from incidental sightings are thought to estimate species distributions as effectively as presence–absence models (Gormley *et al.*, 2011; White *et al.*, 2012). Habitat covariates were derived from Land Cover Map (LCM) 2007 data for the UK (Morton *et al.*, 2011) and presented as the area (hectares) of each habitat type within each 4 km^2 cell. Habitat types were as follows: improved grass, other grass (rough grass + acid grass), heath, bog, littoral rock and supralittoral sediment. Mean elevation (metres above sea level) and length of coastline (metres) per 4 km^2 were also included as covariates. Correlations between covariates were calculated (Spearman's rank correlation; correlated if $r_s \geq 0.6$) but only found

between coast length and littoral rock (r_s = 0.8). These two options for the coastal descriptor were not included in the same model, but were tested separately to see which better explained mink presence. All environmental covariates were standardized to make them comparable. We compared models using the Akaike information criterion (AIC) following backward stepwise selection of individual covariates. To define suitable versus unsuitable habitat within the model predictions, we calculated the optimal threshold for determining the probability of occurrence using the 'required sensitivity' method (PresenceAbsence package in R, Freeman & Moisen, 2008). The habitat suitability model was verified by applying it to a 3300 km^2 island where mink distribution is well characterized by systematic trapping then compared predictions with independent and known distribution of mink on the island. We assessed the observed rate of area expansion in relation to availability of suitable habitat (see Appendix S1).

Testing scenarios for spatial variation by simulating range expansion

We used the habitat suitability model to test scenarios for the expansion of mink throughout Scotland with an individual-based model implemented using the newly available simulation platform, RangeShifter (Bocedi *et al.*, 2014). We modelled dispersal assuming individuals settle stochastically at a distance from their natal site drawn at random from a negative exponential kernel. In cases where the dispersal distance drawn failed to displace the individual from its natal cell, the distance was redrawn and the dispersal distance resampled. Slightly more than half of all dispersal movements were greater than $\log_e(2)$ of the mean dispersal distance parameter value.

Parameters for survival, fecundity and dispersal (the kernel mean) were gained using available empirical estimates and optimized by testing a range of values to best fit the observed modelled distribution in the first seven years of range expansion (see Appendix S1). A variety of hypotheses were tested using different modelling scenarios (Table 1). In scenarios i and ii, all habitat cells had equal value. In scenarios iii–x, habitat cells differed in value and individual productivity was related to habitat suitability. In scenarios iv–x, low quality habitat was redefined as unsuitable. Individuals that dispersed into unsuitable habitat were moved to a suitable neighbouring cell or died if none was available, except in scenario vii where unsuitable habitat was inaccessible. The simulated ranges were compared to observed ranges using the True Skill Statistic (TSS) (Allouche *et al.*, 2006) (see Appendix S1).

RESULTS

Data collection

A total of 5258 records of mink presence were collected, from 1960 to 2012. The number of records from each source (minimum 11, maximum 2023 records) and the time covered by each source (minimum two, maximum 49 years) varied. The number of records varied through time (mean number ± SD of records per five year interval = 478 ± 257), and so, we assigned unequal time intervals with similar numbers of records (without splitting data within years) for analyses. Ten intervals were designated with a mean of 463 ± 99 records.

Calculation of the observed rates of range expansion

Data suggested the spread of mink occurred in three phases: a fast increase in occupied area (1960–1978), a slow, almost stalled advance (1979–1989) followed by a steady increase in occupied area (1990–2012). Relationships between area and time were calculated separately for the three phases. The first and third phases showed a significant linear relationship between occupied area and time (linear regression: phase 1, R^2 = 0.96, P = 0.01, $F_{1,2}$ = 69.15; phase 3, R^2 = 0.97, P = <0.0001, $F_{1,5}$ = 175.4, Fig. 2), and the slopes of the relationships were significantly different (ANCOVA: P = <0.001, $F_{1,2}$ = 46.6). The second phase only had two sampling occasions; therefore, a linear regression statistic was not calculated.

The radial invasion range did not increase with classical linear or exponential patterns for any segment in north-east Scotland (Fig. 3), suggesting that expansion was neither constant nor accelerating. The asymptote reached in segments two and three suggested that the available area was fully colonized by 2003 and 2005, respectively, whereas continual increase in segment one showed that the area is not yet fully colonized. The rate of expansion differed both spatially and temporally. Rates of radial expansion ranged from 1.1 to 22.7 km year^{-1}, with a mean of 9.8 km year^{-1}. In west Scotland, linear expansion rate ranged from 7.8 km year^{-1} to 27.3 km year^{-1}, with a mean of 13.8 km year^{-1}. On the coast in the far north-east of Scotland, linear expansion rate ranged from 1.5 to 4.9 km year^{-1}, with a mean of 2.6 km year^{-1}.

The rate of expansion by area (area of newly occupied ground/time in years) varied temporally (Fig. 4). The rate of expansion by area ranged from 101.1 to 2866 km^2 year^{-1}, with a mean of 1326.9 km^2 year^{-1}.

Modelling habitat suitability within the Scottish landscape

The probability of occurrence of mink in Scotland, according to habitat covariates, was best explained by a positive relationship with area of improved grass and length of coastline, and a negative relationship with elevation, area of other grass types and area of bog (Table 2). The model with the lowest AIC that described mink presence across the whole of Scotland included elevation, improved grass, other grass, bog and littoral rock. However, when this model was applied to west Scotland only, and model predictions were compared with

Table 1 Hypotheses and associated model parameters for simulation models run in RangeShifter (Bocedi *et al.*, 2014). TSS = True Skill Statistic. 'Fit' of TSS values in brackets, as described in Eskildsen *et al.* (2013). Opt. thr = optimum threshold as described in Aben *et al.* (2014)

Scenario	Hypotheses	Habitat suitability	Starting distribution	Fecundity	Mean dispersal distance (km)	Prediction year	TSS (Fit) Opt. thr
i	Range expands at a constant rate when all habitat is equally suitable and fecundity is high	Homogenous – all suitable for establishing a territory	1964	0.6 (constant)	12	2012	0.489 (good) 59
ii	Range expands at a constant rate when all habitat is equally suitable and fecundity is average	Homogenous – all suitable for establishing a territory	1964	0.37 (average)	12	2012	0.527 (good) 2
iii	Variation in the landscape affects rate of range expansion	Heterogeneous – all suitable for establishing a territory	1964	0.6 (maximum)	12	2012	0.539 (good) 5
iv	Simulations can estimate patterns of range expansion in the first phase of invasion	Heterogeneous – some unsuitable for establishing a territory	1964	0.6 (maximum)	14	1978	0.533 (good) 4
v	Simulations can estimate patterns of range expansion in the early stages of the third phase of invasion	Heterogeneous – some unsuitable for establishing a territory	1964	0.6 (maximum)	14	1997	0.454 (good) 4
vi	Variation in the landscape affects rate of range expansion	Heterogeneous – some unsuitable for establishing a territory	1964	0.6 (maximum)	14	2012	0.368 (poor) 4
vii	Range expansion is best estimated by assuming that all unsuitable habitat is completely inaccessible	Heterogeneous – unsuitable habitat is inaccessible	1964	0.6 (maximum)	14	2012	0.378 (poor) 46
viii	Areas in west Scotland were colonized by mink dispersing only short distances	Heterogeneous – some unsuitable for establishing a territory	1964	0.6 (maximum)	6	2164	N/A
ix	All farms known in 1962 contributed to feral mink populations	Heterogeneous – some unsuitable for establishing a territory	Farms in 1962	0.6 (maximum)	14	2012	0.298 (poor) 18
x	Mink populations in west Scotland established from introduction points in west Scotland	Heterogeneous – some unsuitable for establishing a territory	1964 but no points in west	0.6 (maximum)	14	2012	0.370 (poor) 4

those from the model that included coast length as the coastal descriptor, the model with the lowest AIC overpredicted the probability of occurrence of mink on the coast in western areas (it was much higher than reality for areas of known mink presence). Much of western Scotland has a rocky coastline, and so, coast length is more variable than presence of littoral rock in western areas. Although the AIC for this model with coast length as a covariate was higher (ΔAIC = 3.14), the estimates of the coefficients were very similar and so this was chosen as the simplest and best

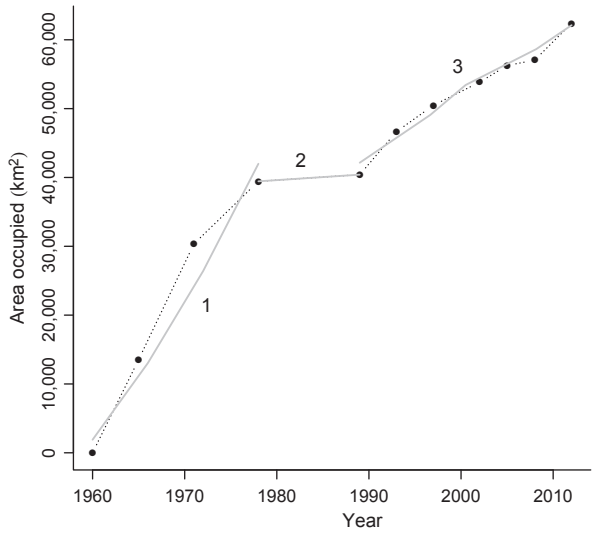

Figure 2 Linear regression of the three phases of invasion: 1 = 1960–1978, 2 = 1979–1989, 3 = 1990–2012.

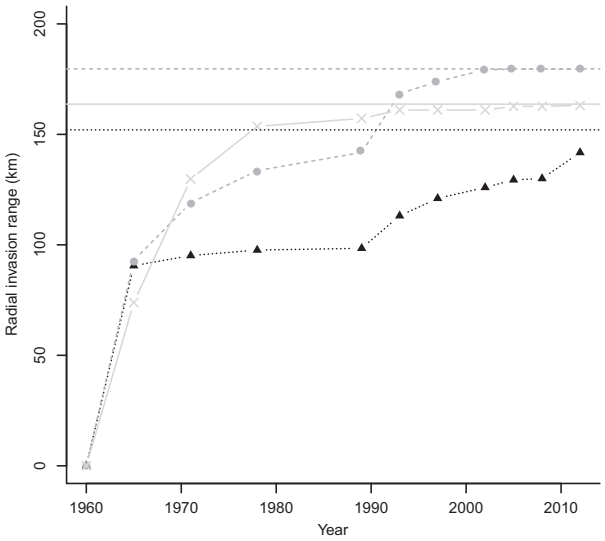

Figure 3 Radial invasion range for three segments in north-east Scotland. Black triangles and dotted line = segment 1, dark grey circles and dashed line = segment 2, light grey crosses and solid line = segment 3. The horizontal lines correspond to the maximum radial invasion range for each segment.

model to predict the probability of occurrence of mink across different areas of Scotland.

The overall predicted mean probability of occurrence was 0.6 (Fig. 5). The optimal threshold for the probability of occurrence was 0.47, at a sensitivity of 0.8. Cells with values <0.47 were deemed unsuitable habitat, and those ≥ 0.47 were considered suitable habitat.

Testing the habitat suitability model

The probability of occurrence for a Scottish island was calculated, with a mean value of 0.5 (see Appendix S2 and Figure S1). Sixty four percent of females trapped on the island were caught in habitat classed as suitable; 36% were in unsuitable habitat. Remembering that the suitability threshold was calculated to account for 80% of presence records, this indicates that the model underestimated habitat suitability for 16% of records on the island.

Relating observed rates of range expansion to habitat suitability

The total newly occupied area significantly decreased over time ($R^2 = 0.62$, $P = 0.004$, $F_{1,8} = 15.96$) as did the proportion of suitable habitat within the newly occupied area ($R^2 = 0.68$, $P = 0.004$, $F_{1,8} = 16.75$).

With regard to radial expansion range, segment three (Fig. 1) had the highest area of suitable habitat which was rapidly, almost completely, occupied by 1993. Segment two had the greatest overall area and the second highest expansion rate despite the lowest availability of suitable habitat. The area of suitable habitat in segment one was the second highest of the three segments but was not fully occupied by 2012. This could explain the recent increase in expansion rate.

The pattern of invasion in west Scotland was primarily latitudinal which corresponded with the distribution of suitable habitat. The mean percentage of suitable habitat in occupied areas in west Scotland (47.7%) was lower than in coastal areas in the far north-east of Scotland (vertical land strip in segment 1, Fig. 1) (67.5%). However, the mean rate of expansion on the coast (13.8 km year^{-1}) was comparably higher than in the north-east area (9.8 km year^{-1}).

Testing scenarios for spatial variation by simulating range expansion

The optimal parameter for fecundity was 0.6 with a probability of juvenile survival at 0.9. The probability of adult survival was optimized at 0.7 and mean dispersal distance at 12 km when all habitat was deemed suitable and at 14 km when some habitat was classed as unsuitable.

The results of all 100 replicates in each model run were plotted but categorized according to the number of times the occupancy of a cell was duplicated. This highlighted areas that were repeatedly colonized in the stochastic simulations and those that were infrequently occupied (Fig. 6).

The model with the highest TSS and therefore the best fit to the observed distribution was scenario iii. The background landscape for this model was heterogeneous, fecundity was scaled to habitat suitability, and individuals were able to settle and breed in all cells. The resulting distribution covered all but the north-west of Scotland. The simulated rate of expansion was clearly affected by landscape as demonstrated by the frequency of occupied cells in eastern compared to western areas (compare Fig. 6i, iii).

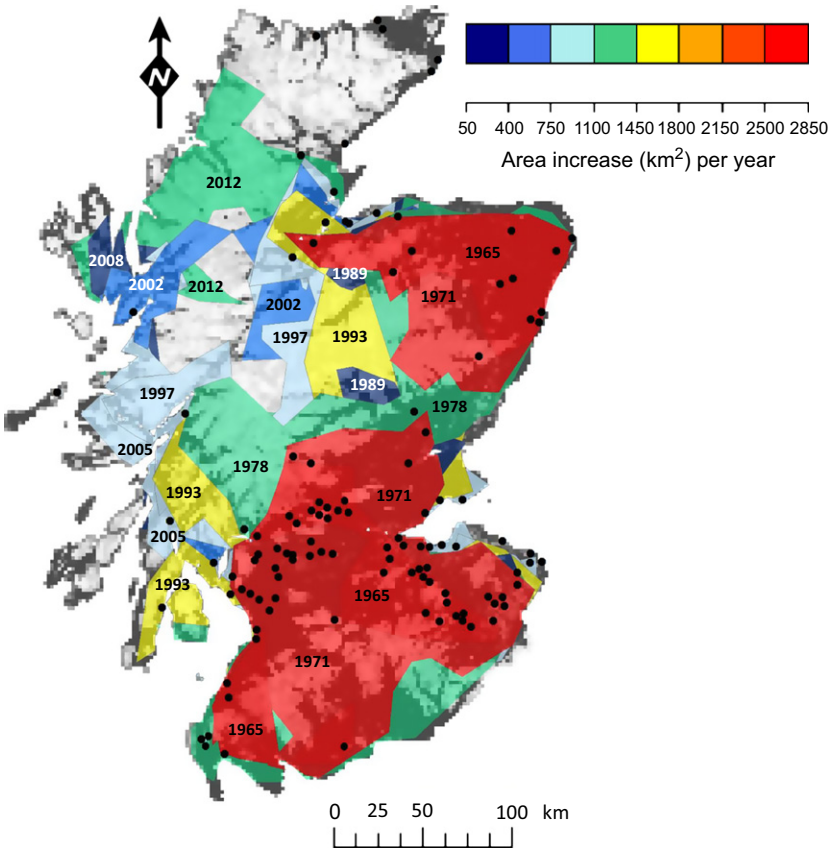

Figure 4 Pattern of mink spread through Scotland, colour coded by rate of expansion (in km^2 year^{-1}), overlaid on a habitat gradient suitability map (see Fig. 5 for further explanation) (black pixels = very suitable, white = very unsuitable). Year dates on the map correspond to the end of the time interval in which the range expanded. Black dots represent locations of known mink farms in 1962. There were initially *c.* 100 farms Scotland-wide, but this decreased to 29 by 1971 after the introduction of the 'Mink Keeping Regulations (Destructive Imported Animals Act 1932)' in 1962 (Cuthbert, 1973).

Table 2 Parameter estimates for the selected 'maxlike' model fitted to the 4141 locations of mink presence in Scotland

Coefficients	Estimate	SE	*Z*	*P*
Intercept	2.815	0.746	3.77	<0.001
Elevation (m)	−0.199	0.094	−2.11	<0.001
Area of improved grass (hectares per 4 km^2)	5.001	1.105	4.53	<0.001
Area of other grass (hectares per 4 km^2)	−0.296	0.068	−4.35	<0.001
Area of bog (hectares per 4 km^2)	−0.289	0.081	−3.57	<0.001
Coast length (m per 4 km^2)	0.424	0.136	3.13	<0.001

SE = standard error; *Z* = Wald statistic; *P* = probability.

Scenarios iv, v and vi presented a time series arising from the same starting conditions, parameter estimates and assumption that low suitability squares could not be occupied as territories. The model fit declined from TSS = 0.53 in 1978 to 0.37 by 2012, suggesting that the assumption of static parameter values may not be appropriate.

TSS values for scenarios vi, vii, ix and x were low suggesting that the simulated distributions were a poor fit with observed distributions (Table 1); thus, scenario hypotheses were rejected.

Mean dispersal distance was reduced to 6 km to see whether a shorter dispersal kernel encouraged settlement in the patchy habitat of western Scotland (scenario viii, Table 1). Repeated occupancy of cells around the south-west introduction point occurred, suggesting that in previous models where 50% of individuals had a natal dispersal distance >9.7 km ($\log_e(2)$*14 km), too many individuals dispersed beyond suitable habitat and died. However, a shorter mean dispersal distance did not promote colonization of north-west areas, even if the model was run for 200 years (Fig. 6viii). A TSS could not be calculated for simulations of future distributions.

DISCUSSION

Records showed that mink were distributed throughout Scotland, except in the far north. We found that the rate of spread varied both spatially and temporally and was related to landscape heterogeneity. In the early stages of invasion, areas of suitable habitat were colonized quickly in comparison to areas of low habitat suitability. By simulating scenarios for range expansion, we concluded that the potential for individuals to disperse long distances does not necessarily facilitate range expansion when availability of suitable habitat occurs in narrow strips and/or is fragmented as is seen in west Scotland.

A precise measure of expansion rate is important for assessing the effect of varied conditions and management practices on the rate of invasion, as well as for contributing to predictions of future invasive species spread (Gilbert &

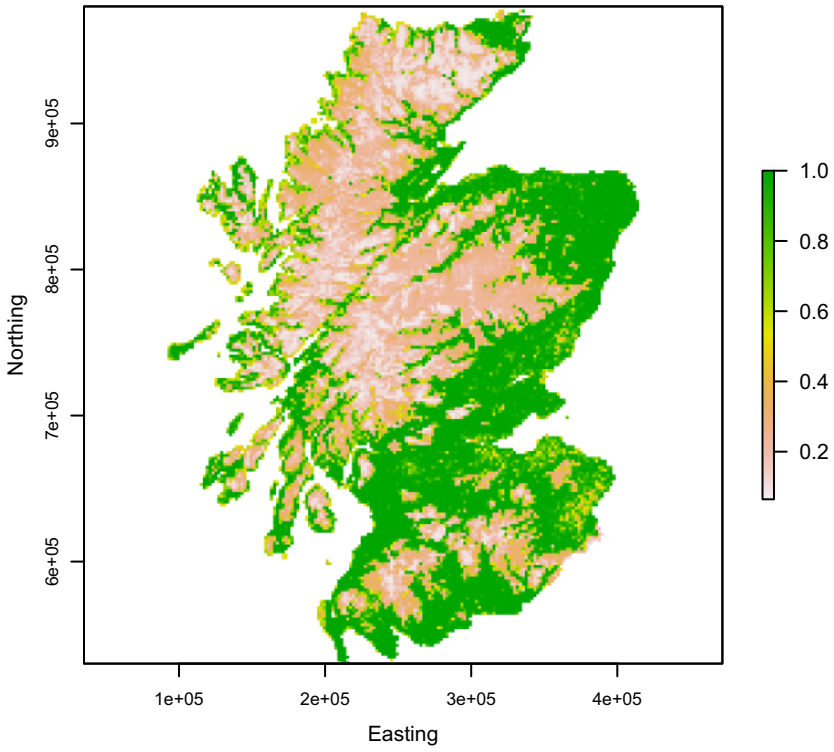

Figure 5 Model predictions for probability of occurrence of mink in Scotland. Green cells indicate a very high probability of mink occurrence, white cells indicate an extremely low probability of mink occurrence.

Liebhold, 2010). There are various methods for calculating the rate of spread (e.g. see Gilbert & Liebhold, 2010), but many rely on assumptions that were not realistic for our dataset. Our method of calculating rate of expansion by the increase in area over time (km^2 $year^{-1}$) allowed comparison of expansion rates within our own dataset. Also, using area, as defined by home range analyses, rather than individual sample points, we minimized the risk of potentially false-positive and false-negative records influencing the observed distribution. Segmented radial range expansion allowed us to sample expansion rates across our landscape for comparison with other studies, but we could not apply this to the whole invaded area due to the multiple introduction points and convoluted coastline that restricted the extent of expansion.

Observed rates of range expansion and modelling habitat suitability

Comparing observed rates of range expansion among years revealed that the initial spread of mink (up to 1971) was the fastest and most extensive. The majority of fur farms were located within this area, and 74% of the occupied land was deemed suitable. As time progressed, the proportion of suitable habitat in each newly occupied area significantly decreased but the rate of invasion did not, perhaps suggesting that mink were colonizing the area by occupying fragments of suitable habitat. Our study did not conform with Jefferies (2003) who reported a contraction in the range of mink from 1990 to 1997.

The mean observed rates of radial invasion in this study are comparable to other studies (e.g. Ruiz-Olmo *et al.*, 1997; Fasola *et al.*, 2011; Iordan *et al.*, 2012), but the upper rate limits in our study far exceeded those reported in all but one other study (Rodrigues *et al.*, 2014). Early rates of expansion in our study were particularly high which could be attributed to high fur farm density and the number of individuals introduced [also known as propagule pressure – a key determinant of invasion success (Jeschke & Strayer, 2006)]. Recent research on mink in Portugal demonstrated slow linear range expansion for the first 20 years (*c.* 2.75 km $year^{-1}$) followed by a rapid expansion over two years (22.5 km $year^{-1}$) (Rodrigues *et al.*, 2014). There were very few fur farms in Portugal, and so, expansion rate was not attributed to propagule pressure. Instead, it was linked with food availability and coincided with range expansion of an introduced crayfish (Melero *et al.*, 2014; Rodrigues *et al.*, 2014). The highest rate of expansion in Spain (10 km $year^{-1}$) did not occur in areas with highest farm density but instead was attributed to habitats with little or no other mustelids (Ruiz-Olmo *et al.*, 1997). Estimated rates for Argentinean Patagonia and Italy were low which may reflect the low number of farms in the study areas (Fasola *et al.*, 2011; Iordan *et al.*, 2012) rather than food availability (Fasola *et al.*, 2011). Previous estimates for range expansion in the UK (Iordan *et al.*, 2012) were much lower than in our study. Iordan *et al.* (2012) calculated the rate of spread within four different 50 × 50 km squares in England over a 14-year period and assumed radial spread from the centre of each square. This was a much smaller scale than ours both spatially and temporally and did not include any major boundaries, for example coastline. It is also unlikely that the selected squares originally included fur farms [the chosen

Figure 6 Summary maps of range expansion simulations. The first map illustrates the distribution of mink in 1964 and was the starting condition for all model scenarios. The observed distribution map illustrates the known cumulative distribution of mink from 1964 to 2012 with an underlying topographical layer, see Table 1 for explanation of parameters and starting conditions of each scenario (i–x). The output maps are colour coded according to the number of times each cell was occupied over 100 model replicates. Black = cells occupied in >50% of 100 model replicates, dark grey = 11–50%, light grey = 6–10%, blue = <6%.

squares did not correspond to areas of early high mink density (see Usher, 1987)]. Propagule pressure does not explain our high rates of expansion from 1990 onwards. This could potentially be attributed to mink moving quickly (i.e. not settling) through areas fragmented with unsuitable habitat. This complements the conclusion reached by Ruiz-Olmo *et al.* (1997) who found that suitable habitat was denser in areas of slow expansion.

Testing scenarios for spatial variation by simulating range expansion

Our model simulations of mink dispersal in Scotland successfully demonstrated range expansion through heterogeneous habitat, bounded by coastline, from multiple introduction points. By simulating range expansion under different scenarios, we were able to test hypotheses for the

most likely causes of variation in expansion rate. The model which best fitted the observation data (scenario iii) had a background landscape that was heterogeneous and fully accessible to mink for forming territories. This suggested that although some areas were less suitable for breeding than others, all areas were 'open' to mink. Unexpectedly, models with a homogeneous landscape (scenarios i and ii) also provided good model fit according to TSS values. Habitat suitability modelling and recent records of mink distribution suggest that there are no mink in the mountainous areas of central and north-east Scotland. However, observed distributions were created from cumulative sightings collected from 1960 to 2012 which resulted in a wide distribution and are likely to include records of pioneering dispersers and transient mink that were recorded in potentially unsuitable habitat. The observed distribution map does not account for areas that have recently been cleared through mink control (e.g. Bryce *et al.*, 2011). This explains why scenario iii was the most statistically agreeable model and also why scenarios i and ii appeared to show good model fit despite having an unrealistic homogeneous landscape. We are confident that the habitat suitability model is a fair representation of the likely current distribution of mink in Scotland and therefore suggest that scenario vi or vii is potentially the most realistic model output. However, at present we are unable to improve our ability to distinguish between models with any degree of confidence using TSS because we do not have sufficiently precise data to determine the exact current distribution. On the basis of the TSS, there was no support for the hypotheses that all known farms in 1962 contributed to feral mink populations (scenario ix) or that introduction points in the west were sources of feral populations (scenario x).

Where suitable habitat was sandwiched between coastline and unsuitable habitat, simulated range expansion was minimal. It is possible that the low availability of suitable habitat restricted the population from increasing enough to push the invasion front northwards. We attributed this to long-distance dispersal movements taking a high proportion of dispersing individuals beyond suitable habitat. The assumed dispersal distances are biologically realistic for mink. A study in north-east Scotland found that only 16% of 64 mink settled within 4 km of their natal site despite many territory vacancies resulting from an intensive culling programme (Oliver *et al.*, 2009; Bryce *et al.*, 2011). By reducing the mean of the dispersal kernel from 14 to 6 km, we demonstrated colonization of south-western areas but not north-western areas. This suggested that shorter dispersal movements kept individuals within the good breeding habitat in areas where it was available inland, but habitat strips in the north-west were still too narrow to be frequently colonized. This implied that, under simulation conditions, the availability of suitable habitat was too small to support an established mink population. We assumed that our habitat suitability predictions were realistic (we showed a good match between model predictions and mink records in the island test case) and so suggest that in reality, unsuitable habitat is not as much of a sink for dispersing individuals as is implied by our simulations.

Lack of observed expansion through the far north-east of Scotland is puzzling. This area demonstrated the lowest rates of expansion, despite predictions in habitat suitability modelling and simulated distributions suggesting that colonization should have occurred. Mink were first recorded in the far north-east of Scotland in 1965 but not again until 1990–1993. There were a handful of farms in this area, but it is possible that early records were isolated cases of escaped mink and that density was not sufficient to allow establishment of feral populations.

CONCLUSIONS

We have highlighted methodological gaps in calculating rates of expansion in invasive species but have demonstrated alternative methods that successfully utilize presence-only data. We have shown that heterogeneity in the landscape affects expansion rate and that simulations of range expansion are improved when landscape heterogeneity is accounted for. We suggest, from results of times series simulation modelling, that it is not always appropriate to assume constant parameters throughout the process of range expansion. We have also shown that long-distance dispersers, often assumed to contribute to the establishment of satellite populations beyond the core of the invasion range (Shigesada *et al.*, 1995), will not necessarily substantially contribute to range expansion when habitat availability is limited, narrow and/or fragmented. Our findings underline the need to remain vigilant of the potential for invasive species expansion, even when the distribution appears to be static. We have shown that suboptimal habitat at the invasion front may only contribute to an expansion lag as opposed to completely restricting range expansion.

For mink in Scotland, we now know that in west Scotland, suitable habitat is primarily restricted to the coastline and that mountainous areas are largely uninhabited by mink. This has important implications for mink management, and we recommend that mink control in west Scotland is focussed in coastal areas. This is supported by a population genetics study which found that populations in western and eastern Scotland were genetically separated and mountains were likely barriers to dispersal (Fraser *et al.*, 2013). We have also shown that expansion rate has varied spatially and temporally but that low availability of suitable habitat has not necessarily decelerated expansion, particularly in coastal areas. We suggest that mink have not yet reached equilibrium in Scotland despite prolonged lags during the spread process. This is despite the fact that the availability of suitable habitat is decreasing with increasing mink range. These findings are not surprising considering mink presence in other countries assumed to be less hospitable, such as Iceland and Norway (Bonesi & Palazon, 2007) but reinforce the idea that mink are adaptable and persistent.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Methods.

Appendix S2 Results.

Figure S1 Testing the maxlike model.

BIOSKETCH

Elaine J. Fraser is interested in applying scientific research to conservation practice, in particular for invasive species management. This study was one aspect of her PhD which researched the management and control of American mink in Scotland. The remaining authors have diverse interests in ecology and conservation and apply a combination of practical and theoretical approaches to conservation and species management.

Author contributions: E.F. collated the data, performed the majority of analyses and led the writing of the paper; X.L., L.H. and D.M. provided advice and support on research design and data analyses; G.B., S.P. and J.T. developed the RangeShifter simulation model and helped apply the model to our data. S.P. also conducted the analyses for TSS.

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